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SEASONAL CHANGES IN SIZE SELECTION AND INTAKE RATE OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* FEEDING ON THE BIVALVES *MYTILUS EDULIS* AND *CERASTODERMA EDULE*

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During the course of spring, Cockles *Cerastoderma edule* and Mussels *Mytilus edulis* grow in size, while the condition, as measured by the biomass content of shells of a given size, also increases. Condition temporarily drops when the larger individuals spawn. This study investigates the effects of these seasonal changes on the intake rate and the prey choice of Oystercatchers. Although profitability (biomass gained per unit time spent handling) was lower when the bivalves were in poor condition, large Cockles and Mussels were always the most profitable. It was therefore remarkable that these large prey were dropped from the diet in spring and early summer. Whereas condition of the molluscs was highest in August, intake rates of Oystercatchers peaked by the end of May, early June, when many adult birds had nests and may have been pressed for time. However, since the intake rate of subadult birds followed a similar seasonal pattern, it seems unlikely that time stress alone caused the adult birds to feed faster. It therefore seems that prey choice is 'suboptimal' in terms of rate maximization when the daily demand for food is minimal and feeding conditions are maximally good. This leads to the suggestion that the prey choice of Oystercatchers in late spring/early summer is more heavily influenced by non-energy criteria like, for instance, the risk of parasitism, than at other times of the year.

Key words: Oystercatcher - *Haematopus ostralegus* - Cockle - *Cerastorderma edule* - Mussel - *Mytilus edulis* - optimal foraging - food intake rate - prey size selection

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INTRODUCTION

Somewhere in early spring the benthic prey that form the staple food for waders in the Wadden Sea, start to grow and reproduce. As a result, those birds that have survived the hardships of winter are faced with a steadily improving food supply. At some stage invertebrate growth and reproduction stop and food supplies decline again due to mortality and loss of condition. According to Beukema (1974), the total benthic biomass varies twofold in the course of the year and reaches a peak in June in the most westerly part of the Wadden Sea. The same pattern was noted by Zwarts & Wanink (1993) for a study area more to the east.

Yet, at the time that the benthic food supplies reach their maximal size, the number of waders exploiting them reaches their annual low (Meltofte *et al.* 1994). As a result one wonders if it is really true that feeding conditions are best when

the biomass of the prey reaches a peak. This would be easy to find out if conditions were simple, i.e. if the birds fed on a single prey species. In that case, we would predict that the seasonal changes in the number and condition of this prey species should closely correlate with the intake rates achieved by the birds. Probably, these ideal simple conditions are rarely met. They certainly do not apply to the Oystercatcher, our study species, for the following reasons:

(1) Although Oystercatchers feed on only a limited number of food items, it rarely happens that only one prey species is on offer (Hulscher 1996). Thus, a way has to be found to combine the various prey into a single measure for the food supply.

(2) When several prey species are on offer individual Oystercatchers tend to specialize, but specializations differ between individuals (Sutherland *et al.* 1996). This means that the annual peak in the food supply may occur at different times of the year for different individuals.

(3) The availability of the prey may depend not so much on the total number of prey present or their profitability, but on burying depth or feeding behaviour of the prey, i.e. on the extent to which prey perform risky behaviour. This may vary greatly during the course of the season (Zwarts & Wanink 1993).

(4) The intake rate of the birds may not only depend on the density of harvestable prey, but also on the time available for feeding. For instance, Swennen *et al.* (1989) have shown experimentally that Oystercatchers can increase their intake rate when stressed for time.

In this paper we report the progress we have made with dealing with these problems in our study of seasonal changes in intake rate and prey choice of Oystercatchers feeding on Cockles and Mussels. From late winter to early summer we made detailed records of the feeding behaviour of adult Oystercatchers, most of which defended nesting territories in the polder close to the study area. We also observed non-breeding subadults, as we expected their feeding behaviour to be less influenced by time stress. In addition, we regularly sampled the Cockles and Mussels to determine their size distribution and condition. Finally, we spent much effort in methodological but important details such as (1) calibrating our field estimates of prey size, (2) validating our field estimates of food intake through comparison with estimates of food intake from weight changes recorded by a balance placed under the nest, (3) calculating the criterion to exclude observation periods that minimizes the bias introduced into estimates of intake rate.

METHODS

Study area

The study was carried out on Texel, the most western island in the Dutch Wadden Sea from February to October 1983 and from February to July 1984. The rather sandy mudflats near the harbour of the Netherlands Institute for Sea Research (NIOZ) served as our study area. At the time it contained several small mussel beds and a few somewhat larger cockle beds. In the summer of 1991 the area more or less ceased to exist due to the enlargement of the harbour. A detailed description of the study area as it was in 1983 is provided by Ens *et al.* (1996). On two sides it was bordered by polders used for agriculture, and for breeding by the Oystercatchers. Many of these breeding Oystercatchers were individually marked. The mudflat study area was divided into 37 squares of 0.25 ha using marker canes (see Fig. 1 in Ens *et al.* 1996). Until July 1983 birds were observed from the dike: from then on we used a hide located at the tip of the stone dike in the centre of the study area.

Sampling minor prey: *Nereis*, *Macoma* and *Carcinus*

Since the Ragworm *Nereis diversicolor*, the Baltic Tellin *Macoma balthica* and the Shorecrab *Carcinus meanas* were rarely taken by the birds (Fig. 8), we devoted relatively little effort to sampling these prey in 1983 and no effort at all in 1984. In 1983 we measured density and size dis-

Table 1. Predicting biomass (W, mg AFDM) from shell length (L, mm) for Mussels in 1983 and 1984, according to the equation $W = \exp(b + a \times \ln(L))$.

	a	b	r	n
1983				
25 April	1.94	-1.20	0.82	39
16 June	2.06	-1.42	0.72	54
5 August	2.26	-1.89	0.83	51
5 Sept.	1.95	-0.85	0.73	55
26 Oct.	2.82	-4.32	0.81	55
1984				
1 Febr.	2.06	-1.71	0.65	40
29 Febr.	2.81	-4.54	0.98	122
10 April	2.61	-3.66	0.99	114
1 May	2.10	-1.92	0.99	138
4 June	1.97	-1.38	0.96	109
9 July	2.63	-3.59	0.98	79
8 August	2.54	-3.29	0.97	88
8 Oct.	2.83	-4.33	0.96	115
21 Nov.	2.89	-4.70	0.98	127

tribution of all animals retained in a sieve with a mesh width of 0.1 mm for selected sites.

Carcinus In late April, early May 1983 we took nine quadrats with a surface area of 0.105 m^2 to a depth of 5 cm in each of the 37 squares comprising the study area.

Macoma In early June 1983 we took five cores with a surface area of 0.0194 cm^2 to a depth of 30 cm in each of 24 squares (A1 to A6, B1 to B6, C1 to C6, D4 to D6, E4, E5, F4) using a flushing sampler (see van Arkel & Mulder 1975).

Nereis In early July 1983 we took five cores with a surface area of 0.0177 m^2 to a depth of 30 cm in each of 13 squares (A1 to A6, B1 to B4 and C1 to C3) where we had sometimes observed birds taking *Nereis*.

Sampling Mussels

Distribution In late April, early May 1983 we sampled all 37 squares comprising the study area, taking nine quadrats with a surface area of 0.105 m^2 to a depth of 5 cm in each of the squares. When densities were very high we took a subsample of half the quadrat. We repeated the procedure in early September 1983 for eleven squares.

Table 2. Predicting biomass (W, mg AFDM) from shell length (L, mm) for Cockles belonging to the year class 1979 or 1983 in 1983 or in 1984, according to the equation $W = \exp(b + a \times \ln(L))$. [1]Correlation coefficient not significantly different from zero.

date	a	b	r	n	soil
year class 1979					
25 April 83	2.38	-2.22	0.93	122	-
15 June 83	2.46	-2.47	0.95	57	-
6 Aug. 83	2.41	-2.25	0.83	61	-
5 Sept. 83	2.68	-3.39	0.78	58	-
27 Oct. 83	3.23	-5.64	0.83	51	-
year class 1979					
19 Febr. 84	2.67	-3.87	0.87	117	-
2 April 84	1.74	-0.60	0.69	68	-
1 May 84	1.86	-0.85	0.75	45	-
5 June 84	1.80	-0.33	0.53	30	-
9 July 84	1.66	+0.15	0.83	10	-
30 July 84	1.44	+1.12	0.65	10	-
8 Aug. 84	2.05	-1.21	0.69[1]	4	-
11 Sept. 84	1.74	-0.15	0.56[1]	9	-
17 Oct. 84	1.58	+0.17	0.31[1]	6	-
year class 1983					
6 Aug. 84	3.04	-5.06	1.00	5	-
5 Sept. 84	2.98	-4.71	1.00	11	-
27 Oct. 84	3.18	-5.45	1.00	8	-
year class 1983					
22 Febr. 84	3.19	-5.72	0.98	12	-
2 April 84	3.28	-5.61	0.95	17	-
1 May 84	2.79	-3.64	0.98	14	-
5 June 84	2.58	-2.88	0.98	16	-
9 July 84	2.77	-3.71	0.90	31	-
8 Aug. 84	3.03	-4.50	0.92	41	-
11 Sept. 84	3.33	-5.31	0.99	87	-
17 Oct. 84	3.57	-6.30	0.99	88	-
8 Aug. 84	3.02	-4.49	0.88	27	sand
8 Aug. 84	3.13	-4.76	0.99	14	mud
11 Sept. 84	3.35	-5.36	0.99	59	sand
11 Sept. 84	3.26	-5.14	0.99	28	mud
17 Oct. 84	3.51	-6.07	0.99	55	sand
17 Oct. 84	3.72	-6.79	0.98	33	mud

Size distribution and biomass content Since most Mussels occurred in square B4, as did most Oystercatchers feeding on Mussels, we decided to take all samples from this site. The global sampling program indicated that the size distribution in B4 was roughly similar to the size distribution in the area as a whole, except that both very small and very large Mussels were more common outside B4 (Fig. 4). In 1983 we collected Mussels on five dates between early April and the end of October to determine the relationship between ash free dry mass (AFDM) and shell length (Table 1) using standard procedures (see e.g. Zwarts 1991). In 1984 we collected Mussels from two quadrats with a surface area of 0.105 m^2 in B4 every month, starting in February and ending in November. We lumped the samples to obtain a single size distribution and to determine the relationship between AFDM and shell length (Table 1).

Sampling Cockles

Distribution In late April, early May 1983 we sampled all 37 squares comprising the study area, taking nine quadrats with a surface area of 0.105 m^2 to a depth of 5 cm in each of the squares. We repeated the procedure in early September 1983 for eleven squares.

Size distribution and biomass content Since the global sampling program indicated that the size distribution of old Cockles differed between the muddy and the sandy sites, we decided to take regular samples from A6 and D4 on five dates between early April and the end of October 1983. We used the Cockles to determine the relationship between ash free dry mass (AFDM) and shell length (Table 2). In 1984 we collected Cockles from quadrats with a surface area of 0.105 m^2 in B1 and D4 every month, starting in February and ending in November. Initially, we also sampled A6, but since cockle densities became very low by the end of June, we switched to B3. We used the samples to obtain a size distribution and to determine the relationship between AFDM and shell length (Table 2).

Feeding behaviour

Diet scans Between March 1983 and November 1984 we tried to spend at least one entire tide per month scanning the study area and noting for each marked bird in which square it was feeding and what prey it was taking.

Feeding observations If possible, we selected a marked bird as focal animal. Observations of focal animals either lasted 10 minutes (10 min records), an entire low water period or in a few cases the entire daylight period (long records). For these long records, the observation period was also divided into bouts lasting 10 minutes. We observed the birds from a hide using a telescope with a magnification of between 20× and 40×; focal birds rarely fed at distances exceeding 150 m. If the bird was marked we noted its code, which allowed the determination of age and breeding status. For unmarked birds we could only deter-

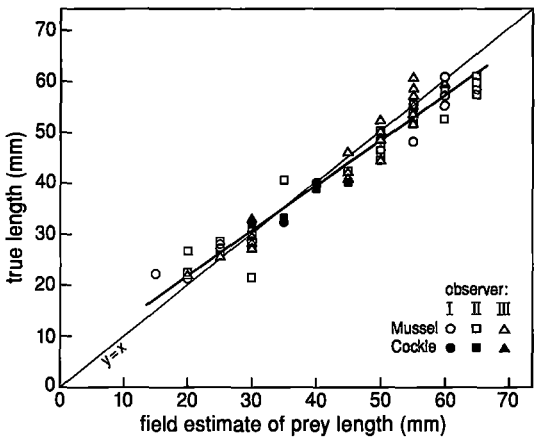


Fig. 1. Relating the true shell length of Mussels and Cockles to their estimated length for three different observers in 1984. In an ANCOVA with true length as the dependent variable, there was no significant interaction between estimated length and observer: $F_{2,78} = 2.66$, $p = 0.08$. In the subsequent model with a fixed common slope there were no significant differences between observers: $F_{2,80} = 1.14$, $p = 0.32$. Lumping observers, length (L, mm) could be predicted from the estimated length (E, mm) as follows: $L = 0.88E + 4.2$, $R^2 = 0.95$, $n = 84$, $p < 0.0001$.

mine age. At the start and end of each 10 min record we noted the square where the bird was feeding, the number of feeding and resting Oystercatchers in the square, the proportion of the surface area of the square that was exposed and the number of disturbances during the observation period. One observer watched the bird, while the other typed the data on feeding behaviour into an OS3 event recorder (Observational Systems Inc, Seattle), which allowed transference of the data to a mainframe computer. For the time budget we distinguished the following behaviours: searching, handling prey, various types of aggression, various types of nesting activities, walking, looking, flying, preening and sleeping. When a prey was caught we noted the prey species, the size of the prey (for bivalves we estimated the length of the shell in 5 mm classes using the colour rings of known length as a reference, for worms we estimated the length relative to the length of the bill and classified the worm as slender, of average width or broad), the method of handling the prey (for bivalves only: stabbed, hammered dorsally or hammered ventrally) and an estimate of the proportion of the prey that was consumed (some prey were partly lost due to robbing, while on other occasions prey were abandoned). On some occasions we noted the time it took the bird to take 50 paces during feeding.

Converting size estimates into biomass ingested According to Goss-Custard *et al.* (1987) mussel length can be estimated reliably as long as the observer's individual bias is taken into account. When Ens (1982) related his size estimates of Mussels to the real length of those shells he could later relocate in the field, he found that the bias was minimal. The same conclusion can be drawn from a calibration experiment in 1984, where Mussels were held next to a model Oystercatcher. There were no significant differences between the three observers in this experiment (Fig. 1). In a few cases we could not estimate the length of the Mussel and in that case we classified the Mussels as small, medium or large on the basis of the size of the flesh that the bird extracted. Looking at the distribution of sizes taken we assigned the following lengths: 20 mm to small, 35 mm to medium and 50 mm to large Mussels.

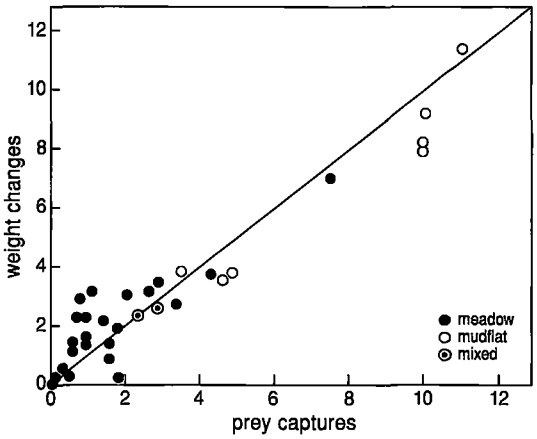


Fig. 2. Food intake as estimated from direct observations plotted against food intake as estimated from weight changes recorded by a balance placed under the nest of the Oystercatcher pair WEWL and LYKY in the 1984 breeding season. Each dot indicates a feeding bout of one individual and different symbols indicate different diets, depending on the feeding habitat. The line $Y = X$ is depicted as the slope of the linear regression did not differ significantly from 1: $t = -0.137$, $df = 27$, $p = 0.9$.

Whereas we could nearly always see the shell of the Mussels that were taken, Cockles often remained buried during consumption. However, since only two year classes occurred in the study area (very big Cockles from 1979 and very small Cockles from 1983, see later) it was always easy to tell whether the Cockle was small or large. Since size differences within a year class within a square were small, and since Leopold *et al.* (1989) found no substantial selection for size under such conditions, we decided to estimate cockle size from the average length of the particular year class in the particular square. These sizes were known from the sampling program.

For worms we also performed a calibration experiment where worms were held next to a model Oystercatcher. We later determined the AFDM of the worms used in the experiment.

There were no systematic differences between observers (Nieuwenhuizen unpubl.).

For worms, the calibration curves allowed a direct transformation of the worm size estimates into AFDM. For Cockles and Mussels we first needed to assign to each shell length a biomass value on the basis of the relationships in Tables 1 & 2. We used linear interpolation when the observation date was between two dates on which the relationship between shell length and biomass was determined (see Figs. 5 & 7).

Observations on a pair of Oystercatchers breeding on a nest under which we had placed a balance allowed a validation of our estimation procedures (Nieuwenhuizen unpubl.). Following the methodology outlined by Kersten & Visser (1996) we could estimate the total amount of food ingested during a feeding bout. There was a good correlation between food intake as estimated from direct observations and as estimated from the nest balance (Fig. 2).

Data analysis We later added to each 10 min record the height of the tide in the NIOZ-harbour, estimated from the continuous records made by Rijkswaterstaat in Oudeschild. Comparing our readings of the tide-gauge in the NIOZ harbour to the records from Oudeschild we found that Oudeschild lagged 20 minutes behind. Taking this time difference into account, tide height in the study area (Y) could be calculated from the tide height at Oudeschild (X) using the following equation:

$$Y = 8.09 + 0.824X,\ r = 0.98,$$

where both X and Y are expressed in cm relative to NAP.

There were often 10 min periods during which the individual foraged for only part of the time, especially when we followed an individual throughout an entire low water period. Since inclusion of periods with very short foraging times might bias the results we looked for an objective criterion to exclude observation periods. To this end we plotted for 25 days during which we followed an individual throughout the entire low water period, the intake rate calculated as the total food consumption divided by the total time spent foraging against the average over the selected 10 min periods. Without selection the correlation was poor and there was a clear indication that including all periods would bias the results towards a low intake rate (Fig. 3). Excluding 10 min periods with less than 120 s foraging removed the bias and yielded a very good correlation. Making the selection criterion even more severe did not lead to further improvement. In fact, matters became worse when the criterion was set at 300 s. Thus, we decided to include all 10 min periods

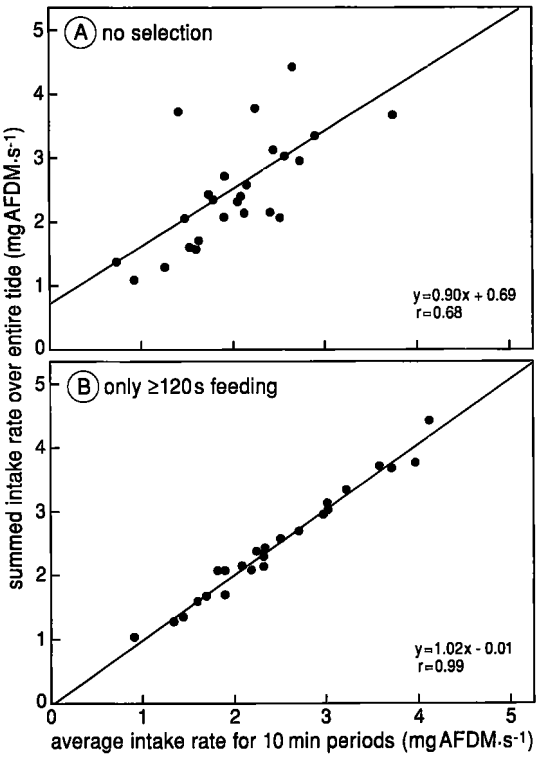


Fig. 3. Intake rate, calculated from total food intake over a tide divided by total time spent foraging, plotted against the average intake rate from selected 10 min periods for the same tide ($n = 25$); data from 1984. (A) No selection: $Y = 0.90X + 0.69$, r = 0.68. (B) Excluding 10 min periods with less than 120 s foraging time: $Y = 1.02X - 0.01$, $r = 0.99$.

during which the bird was foraging for at least 120 s.

We employed Pascal programs to create two data files. One where each case represented the time budget and food intake per 10 min period and one where each case represented the data per prey item that was captured. To analyse the data we employed the statistical software package SPSS (Norusis 1988). When analysing seasonal trends in intake rate and pace rate, we concentrated on the 10 min records, as it seemed relatively safe to treat each as an independent observation.

RESULTS

Mussels

Size distribution In April 1983 nearly all Mussels measured between 35 mm and 50 mm (Fig. 4). At the end of the growing season, the distribution had shifted approximately 5 mm to the right. This was also the size distribution encountered by the birds in the late winter and early spring of 1984. However, during the course of that season the old Mussels became overgrown with small Mussels and had virtually disappeared by the end of that year. We do not know what caused this redistribution of small Mussels, which were more common outside B4 in 1983 (Fig. 4), in the early spring of 1984.

Biomass content The equations in Table 1 allow us to calculate how the biomass content of a Mussel of a given size changes in the course of the season (Fig. 5). In both years condition peaked in July, while minimum weights were reached in late winter, as is typical for Mussels in the Wadden Sea (Zwarts & Wanink 1993). In May 1984 weights dropped dramatically, probably due to

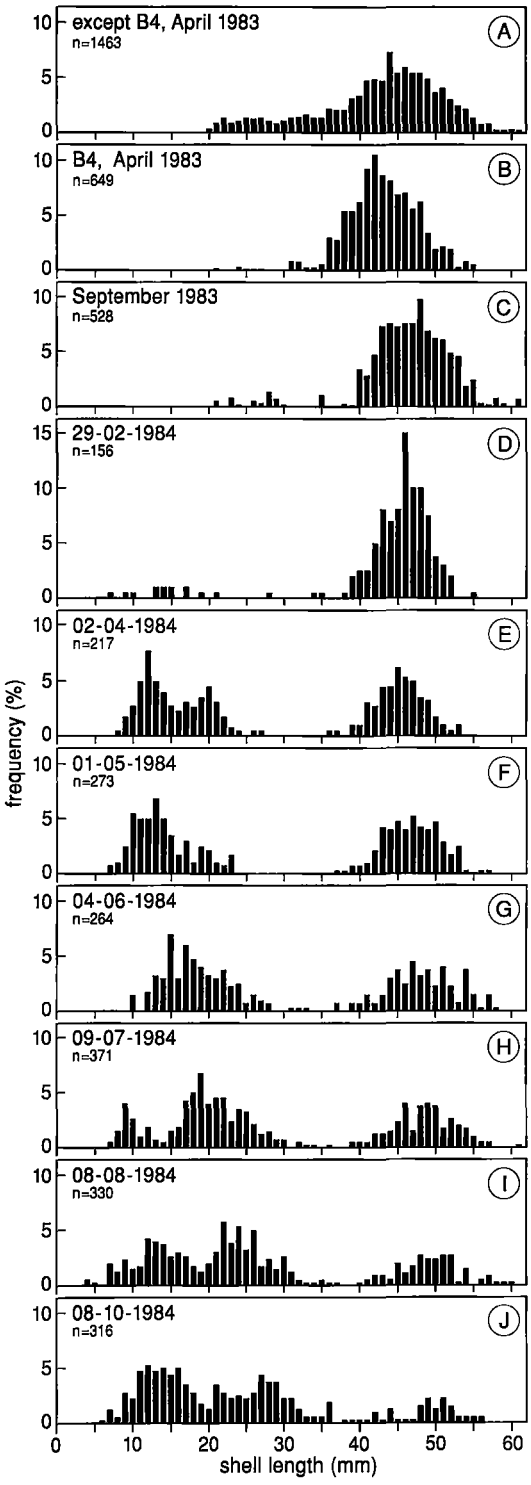


Fig. 4. Size distribution of Mussels in square B4, which contained the mussel bed, for April 1983, September 1983 and seven dates in 1984. For April 1983 the size distribution in the other squares is also given, to allow a comparison with B4.

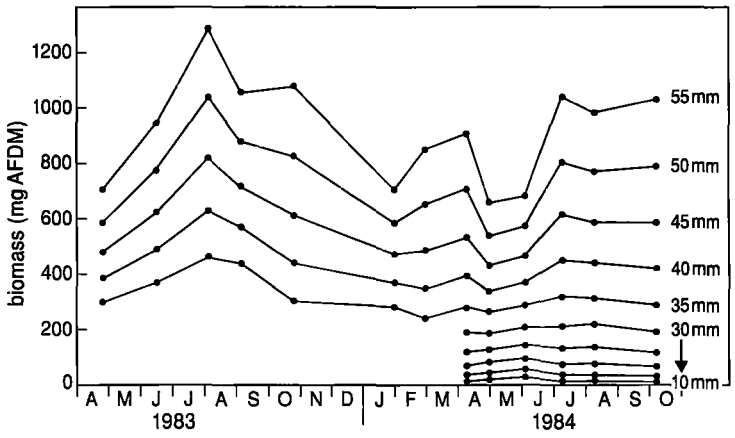


Fig. 5. Seasonal change in the biomass content of Mussels of a given size for 1983 and 1984, calculated from the data in Table 1.

spawning (see references in Zwarts & Wanink 1993). Because we did not sample in the early spring of 1983, we do not know if the Mussels in May 1983 were also recovering from a temporary weight loss.

Cockles

Size distribution Two year classes of Cockles occurred in the study area: very large and very small Cockles (Fig. 6).

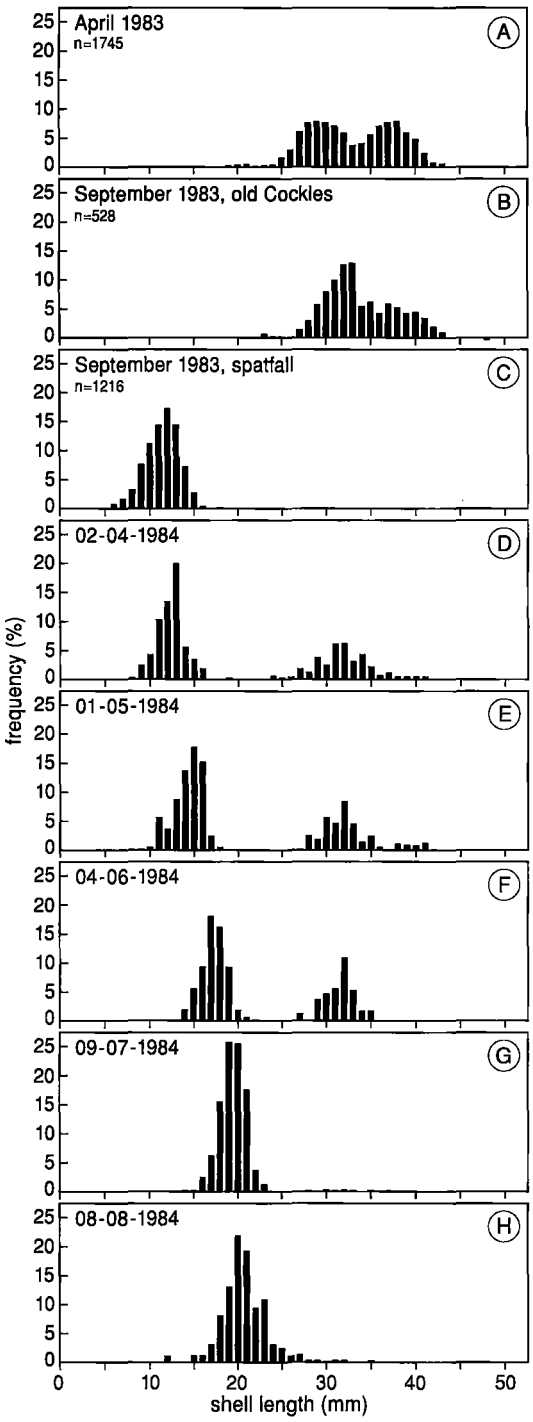
The very large Cockles almost certainly originated from the heavy spatfall of 1979, following the severe winter in 1978/1979. Massive spatfall of several bivalve species was recorded throughout the Wadden Sea in that year (Beukema *et al.* 1993). As bivalves grow older and larger their growth rate tends to decrease (e.g. Wanink & Zwarts 1993) and the large Cockles in our study area were no exception: in 1983 shell growth over the entire season varied from 2 mm for the smaller specimens of around 30 mm, which occurred in the high and muddy parts of the study area, to less than 1 mm for the larger specimens of around 38 mm, which occurred in low and sandy parts of the study area (see also Ens *et al.* 1996). The size differences do not contradict the suggestion that the large Cockles were from a single year class, since Cockles grow better on low-lying sandy mudflats (Wanink & Zwarts 1993). In 1984, growth of large Cockles was again negligible, but very few large Cockles remained by the end of the summer.

The small Cockles were from a spatfall that occurred in the summer of 1983. This spatfall was most intense in the central part of the study area where there were few large Cockles. By the end of the year the Cockles had grown to sizes ranging from 5 to 15 mm. In 1984, growth of shell size took off in April and continued until September (Fig. 6).

Biomass content In both years, biomass content of old Cockles peaked in July-August and reached minimum values in winter (Fig. 7). Although this pattern fits the general pattern described by Zwarts (1991) for the Wadden Sea, he finds that the peak biomass tends to occur in June. Remarkably, biomass content peaked at a much higher value in 1983 compared to 1984. Both young and small Cockles seemed to experience a temporary decline in biomass growth during June, probably due to spawning (see references in Zwarts 1991).

Diet

Seasonal changes Throughout both 1983 and 1984 Mussels and Cockles were by far the most important prey species: alternative prey, includ-



ing Baltic Tellins, Periwinkles *Littorina littorea*, Shorecrabs, Lugworms *Arenicola marina* and Ragworms never made up more than 30% of the diet (Fig. 8). However, the importance in the diet of either Cockles or Mussels varied considerably. Alhough very important in March 1983, Cockles disappeared completely from the diet in spring 1983, only to reappear again in late summer and becoming a very important prey in winter. Usage of Cockles declined in the spring of 1984, but unlike the year before, Cockles were not completely dropped from the diet. This was found to be due to the appearance of the small Cockles. In line with the general finding that one year old Cockles tend not to be taken by Oystercatchers due to their low profitability (Zwarts *et al.* 1996, see also Fig. 12) we observed very few Oystercatchers taking these small Cockles in 1983. From February 1984 onwards small Cockles were increasingly often taken, which we had to infer from the feeding observations, as we did not note during the scan observations whether large or small Cockles were taken (Fig. 9). Using these estimates it is clear that large Cockles were completely dropped from the diet in the course of the spring and early summer of 1984, just as in 1983.

Mussels were especially common in the diet in summer in both 1983 and 1984. However, the switch to Mussels was less marked in 1984, due to the inclusion of small Cockles in the diet (Fig. 8). When the size of Mussels is taken into account it is clear that the Oystercatchers switch to feeding on smaller Mussels in the course of spring 1984 (Fig. 9).

Fig. 6. Seasonal change in the size distribution of Cockles. The two top panels give the size distribution of the Cockles from the year class of 1979 for April and September 1983, respectively. The third panel gives the size distribution of the spatfall in September 1983. In the lower panels for 1984 the combined size distribution is presented.

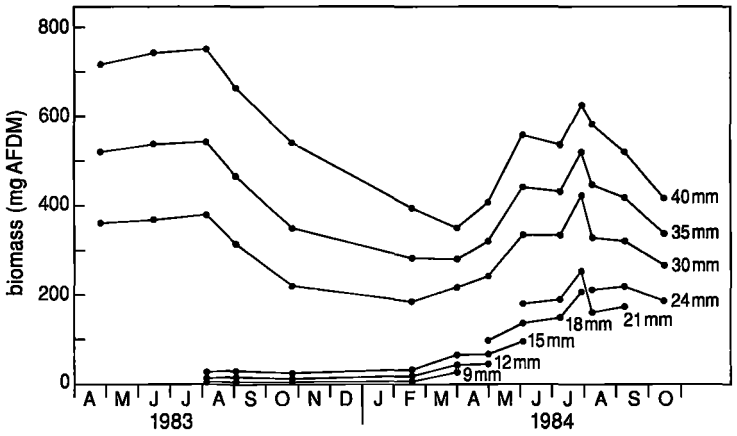


Fig. 7. Seasonal change in the biomass content of Cockles for 1983 and 1984. Only size classes that were actually present in the study area are represented.

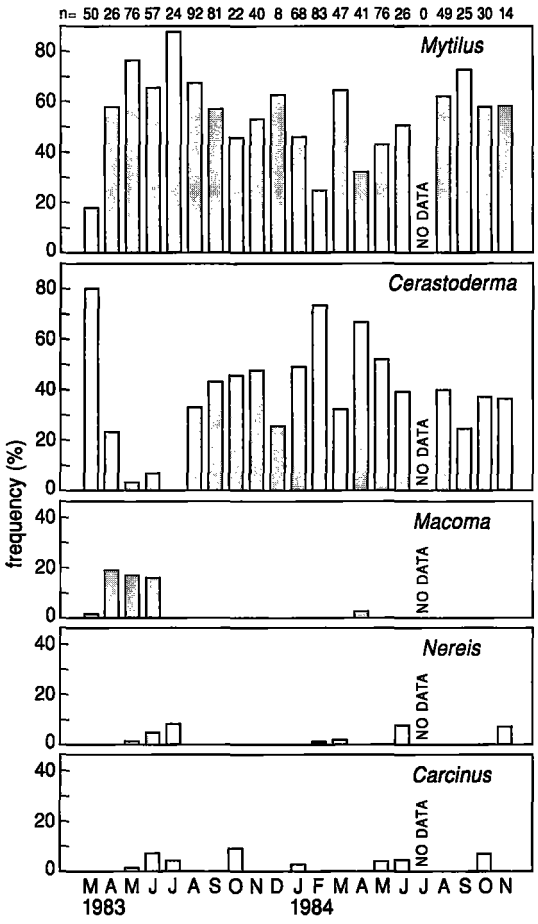


Fig. 8. Diet (prey items, %) in the course of the season as inferred from scan observations in 1983 and 1984.

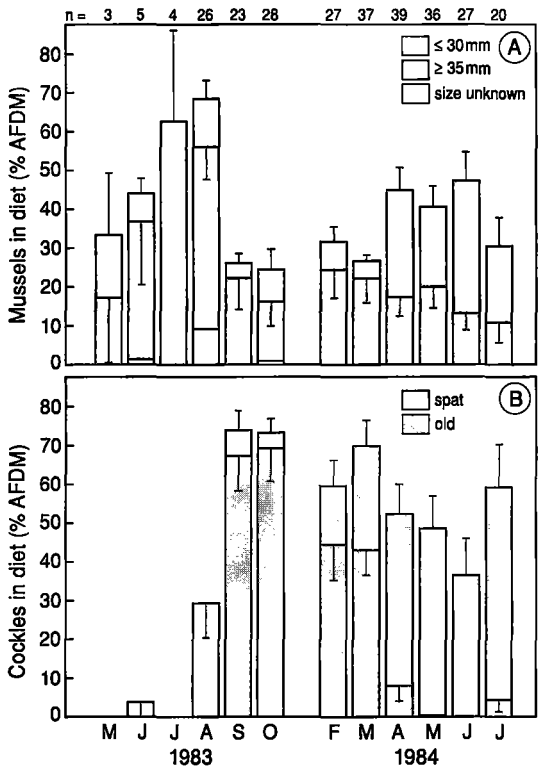


Fig. 9. Diet (biomass, %) in the course of the season as inferred from feeding observations in 1983 and 1984. Sample sizes refer to the number of feeding observations, while bars represent *SE*.

Individual specializations The Oystercatcher is renowned for its habit of specializing on particular prey types and particular methods of opening the prey (see review by Sutherland *et al.* 1996). When individuals were followed over short periods they usually fed on only one of the two staple foods, i.e. Cockles or Mussels, which they either hammered or stabbed. However, it seems unlikely that these specilizations were absolute, since the probability that an individual was observed to take both prey increased with the total number of prey taken (Fig. 10). Similarly, among those individuals observed to take many prey, there were no individuals that only hammered and only a minority that only stabbed their prey (Table 3).

Even though feeding specializations were not absolute, it was important to check that the diet switch applied to individual birds instead of birds with different specializations moving in and out of the study area. We therefore divided our observations on each individual into a 'summer' period

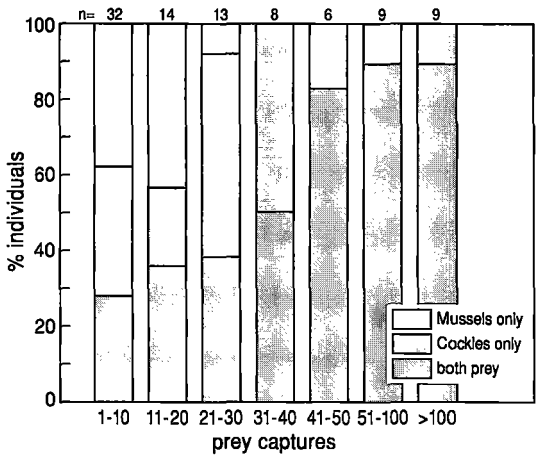


Fig. 10. Probability that an individual took only Mussels, only Cockles, or both prey as a function of the total number of prey captures that we observed. Numbers represent the total number of individuals per class. Data from 1983 and 1984 are lumped.

Table 3. Prey choice (%) and feeding method (%) for 18 Oystercatchers that took more than 50 prey items during the study period.

code	sex	Cockle		Mussel		*n*	Cockle			Mussel		
		yng	old	yng	old		stab	hammer	*n*	stab	hammer	*n*
LWBR	♂	0	0	65	35	206	100	0	1	100	0	201
LWHB	♂	73	2	13	12	379	69	31	279	70	30	69
LWLY	♂	36	15	7	43	182	89	11	56	100	0	47
LWPR	?	49	11	40	0	93	100	0	55	43	57	37
LYKY	♀	62	11	24	3	111	49	51	80	23	77	30
RWAB	♂	1	7	56	35	454	28	72	36	86	14	387
RWAR	♀	94	0	5	2	62	74	26	58	100	0	4
RWAW	♂	16	43	11	30	82	23	77	43	35	65	34
RWAY	♀	24	76	0	0	55	25	75	51	-	-	0
RWKB	♀	84	7	7	2	435	38	62	339	34	66	35
RWQY	?	78	0	20	2	111	100	0	87	100	0	24
RWTR	?	82	0	18	0	78	100	0	64	100	0	14
RWTW	♂	100	0	0	0	106	99	1	106	-	-	0
WEWE	♂	87	0	8	5	61	21	79	53	0	100	8
WEWL	♂	90	2	5	3	631	99	1	580	94	6	50
WEWN	♂	61	0	34	5	76	16	84	45	34	66	29
WHWJ	♀	83	7	10	0	81	47	53	73	0	100	8
WHWN	♀	21	4	73	2	56	100	0	14	100	0	42

Table 4. Size selection and season for individual Oystercatchers that took at least ten Cockles (or Mussels) in both 'summer' (April, May, June and July) and 'winter' (remaining months). Cockles of the year class from 1979 were classified as large and those from 1983 as small. Mussels were classified as large when they exceeded 30 mm in length. Comparing all individuals, irrespective of prey type showed that size selection differed between the two seasons: Wilcoxon matched-pairs signed-ranks test $Z = -2.55$, $p = 0.01$.

individual	sex	winter		summer	
		%large	*n*	%large	*n*
Mussels					
RWAB	♂	63	82	33	315
LWBR	♂	44	149	11	56
LWHB	♂	42	38	44	23
WHWP	♂	10	10	0	19
Cockles					
RWAY	♀	100	42	0	13
WEWL	♂	43	21	1	558
RWKB	♀	36	83	0	312
LWLY	♂	31	82	20	10
LWPR	?	25	36	5	20
RWTR	?	0	29	0	35
RWTW	♂	0	56	0	50
WBWJ	♂	0	11	0	25
WEWN	♂	0	26	0	20

(April, May, June and July) and a 'winter' period (the remaining months). It turned out that there remained only nine individuals for which we had at least ten observations on the size of Cockles taken in both winter and summer, while only four individuals met the selection criterion for Mussels. No individual met the selection criterion for both prey. Despite the small sample size there is positive evidence that the majority of individuals fed on smaller prey during 'summer' (Table 4).

Thus, Oystercatchers switched to feeding on the smaller individuals of both Cockles and Mussels during the course of spring. Since large Cockles and Mussels are the most profitable (see later) this is rather surprising. In the following we will analyse the seasonal changes in the feeding behaviour of the Oystercatcher in more detail in an attempt to provide an explanation for this phenomenon.

Profitability of the prey

For both Cockles and Mussels handling time increased with shell size (Figs. 11, 12 & 13). Furthermore, handling time was higher when the bivalves were hammered instead of stabbed (due to small sample sizes Mussels that were hammered ventrally were lumped with Mussels that were hammered from the dorsal side). Finally, for each

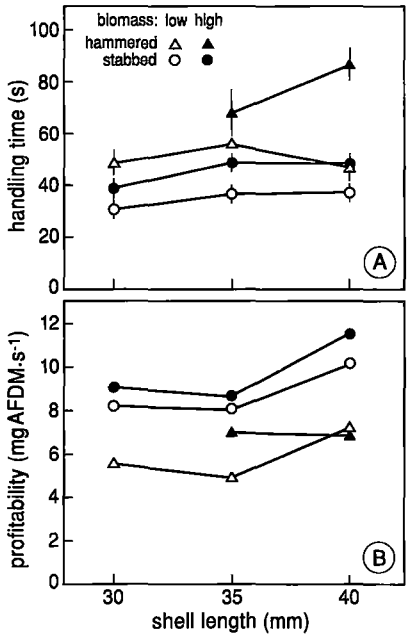


Fig. 11. The effect of shell size, biomass content and feeding method on the handling time and the profitability of large Cockles of the year class of 1979. (A) Handling time (s, bars represent *SE*) and (B) profitability (mg AFDM s^{-1}) plotted against shell size (mm), separated for Cockles that were hammered or stabbed and with a low or high biomass content. An ANOVA showed that handling time was significantly affected by method (classified as hammering or stabbing) and condition (classified as below average or above average) as main effects and size as covariate ($p < 0.001$). The interaction between condition and method was also significant ($p = 0.001$). Data from 1983 and 1984 are lumped.

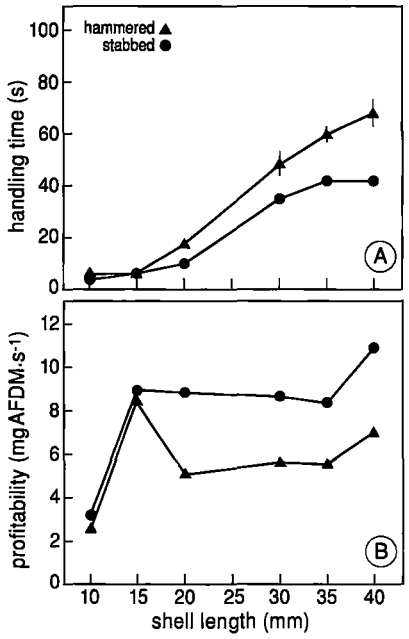


Fig. 12. The effect of shell size and feeding method on the handling time and profitability of Cockles, irrespective of biomass content and year class. (A) Handling time (s, bars represent *SE*) and (B) profitability (mg AFDM s^{-1}) plotted against shell size (mm), separated for Cockles that were hammered or stabbed. Data from 1983 and 1984 are lumped.

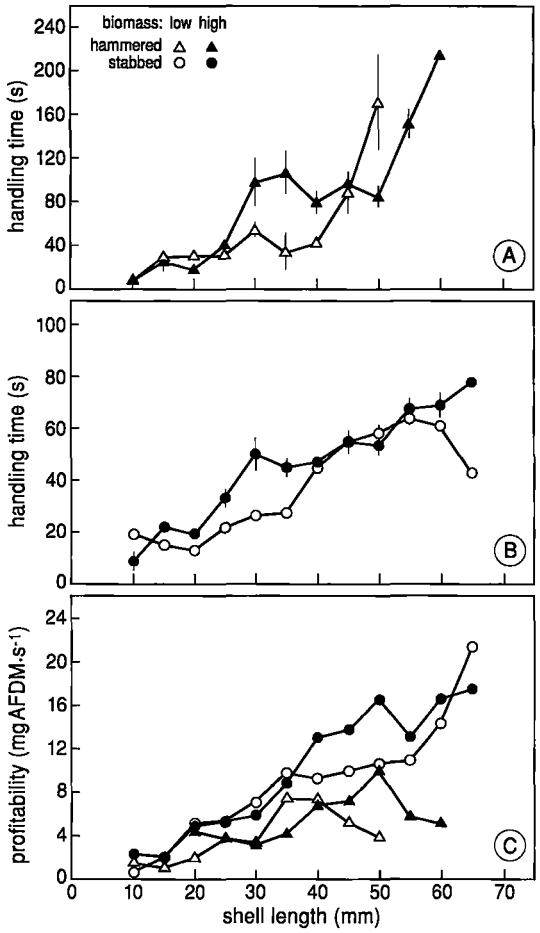


Fig. 13. The effect of shell size, biomass content and feeding method on the handling time and the profitability of Mussels. (A) Handling time (s, bars represent *SE*) for hammered Mussels, separated for Mussels with a low or high biomass content, (B) handling time (s, bars represent *SE*) for stabbed Mussels, separated for Mussels with a low or high biomass content, and (C) profitability (mg AFDM s^{-1}) plotted against shell size (mm), separated for Mussels that were hammered or stabbed, and with a low or high biomass content. An ANOVA showed that handling time was significantly affected by method (classified as hammering or stabbing) and condition (classified as below average or above average) as main effects and size as covariate ($p < 0.001$). The interaction between condition and method was also significant ($p = 0.02$). Data from 1983 and 1984 are lumped.

prey class the average biomass content for all observations was calculated. Subsequently, individual prey could be classified as containing below average or above average biomass. For both Cockles (Fig. 11) and Mussels (Fig. 13) handling time significantly increased with the condition of the prey when variations in shell length and handling method were taken into account. Profitability was calculated as the average biomass of a class divided by the average handling time for that class. Not surprisingly, profitability was reduced when the time-consuming hammering instead of stabbing was used (Figs. 11, 12 & 13). Profitability increased with shell size, but the effect was much more pronounced in Mussels (Fig. 13C) than in Cockles (Fig. 12B). The increase in

Table 5. Intake rate (mg AFDM s^{-1}) as a function of breeding status for birds whose nesting territory was regularly checked for nests in 1984. Sample size refers to the number of 10 min periods (long records excluded). A one-way ANOVA indicated that the differences were highly significant: $F_{3,83} = 5.1, p = 0.003, R^2 = 0.15$.

status	$\bar{x}$	*SE*	*n*
before breeding season	2.0	0.2	54
< 3 wk before first egg	3.0	0.6	12
eggs or chicks	3.5	0.4	12
clutch or brood lost	2.6	0.4	9

biomass apparently more than offset the increase in handling time associated with an increase in condition of the bivalves, so that profitability tended to be higher when the bivalves were in good condition (Figs. 11B & 13C). Although the increase in profitability was not very large, it decisively refutes any suggestions that large bivalves might be dropped from the diet in spring as a result of a reduction in profitability.

Intake rate

One might expect that selection against the most profitable size classes during spring would have a negative effect on intake rate. Remarkably, intake rates were highest during this time of year and this was true for both prey species (Fig. 14). Since it has been experimentally demonstrated that Oystercatchers can increase their intake rate when stressed for time (Swennen *et al.* 1989), the peak in intake rate might be related to the need to attend the nesting territory during the breeding season. Certainly, adult breeders spent increasingly less time on the mudflats as the breeding season progressed (Fig. 15). It was also true that intake rates were highest in the three weeks preceding the first egg and when the birds were actually caring for eggs or chicks (Table 5). However, birds in their second and third calendar year do not breed and yet the intake rates of these birds seemed to follow a similar seasonal pattern to that of the adults (Fig. 14). Due to their lower feeding skills we would expect the intake rates of the immatures to be lower than those of the adults (Goss-Custard & Durell 1987). Although this was true on 12 out of 15 tides where a sufficient number of 10 min records was collected to make the

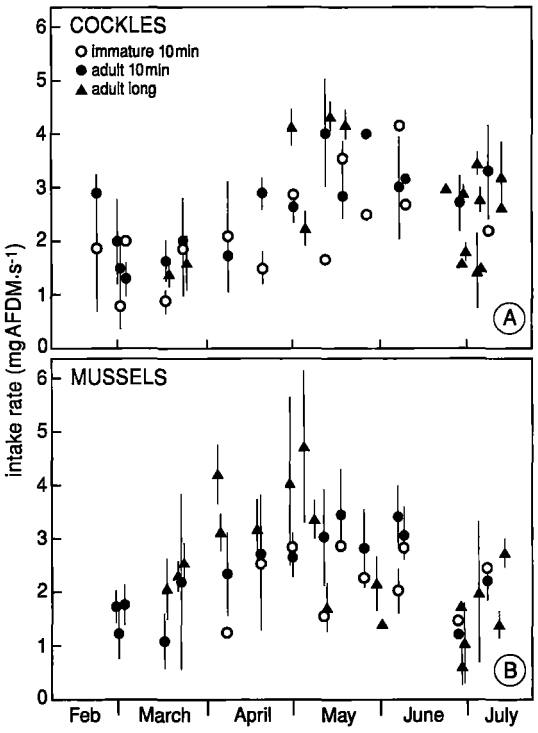


Fig. 14. Intake rate in the course of the season of 1984 for Oystercatchers feeding on (A) Cockles, and (B) Mussels. Closed circles indicate adults (79 and 55 10-min records for Cockles and Mussels, respectively) and open symbols indicate immatures, i.e. birds in their second and third calendar year (24 and 16 10-min records for Cockles and Mussels, respectively). Also indicated with triangles are records for breeding adults followed throughout a whole tidal cycle. Each dot represents the average for a tide (bars give 1 *SE*, which for the 10 min records represents the error between individuals and for the long records the error within an individual). A three-way ANOVA for the 10 min records with age (immature or adult), prey type (Cockle or Mussel) and season (categorized as month) as main effects showed that only season significantly affected intake rate: $F_{1,162} = 7.2, p < 0.001, R^2 = 0.18$; none of the interactions was significant.

Table 6. Pace rate (calculated as steps per s from the time it took a feeding bird to take 50 steps during feeding) as a function of season (March till July) and prey type (Cockles or Mussels). Sample sizes refer to the number of 10 min periods in 1984 (long records excluded). A three-way ANOVA on pace rate, which also included age (immature or adult) as main effect indicated that only month ($F_{4,115} = 2.9, p = 0.03$) and prey type ($F_{1,115} = 20.0, p < 0.001$) had a significant effect, while none of the interactions was significant. In the two-way ANOVA both main effects remained significant (month: $F_{4,124} = 2.9, p = 0.03$; prey type: $F_{1,124} = 20.5, p < 0.001$), but so was the interaction: $F_{4,124} = 2.5, p < 0.05$. One-way ANOVA's for each prey type separately indicated that this was due to the fact that birds feeding on Cockles changed their pace rate in the course of the season ($F_{4,71} = 4.7, p < 0.005$), while birds feeding on Mussels did not do so ($F_{4,53} = 0.9, p = 0.48$).

month in 1984	Cockles			Mussels		
	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	*n*
March	1.9	0.1	22	1.2	0.2	6
April	1.6	0.1	19	1.5	0.1	18
May	1.6	0.1	17	1.3	0.1	12
June	1.8	0.1	10	1.5	0.1	16
July	2.3	0.2	8	1.4	0.2	6

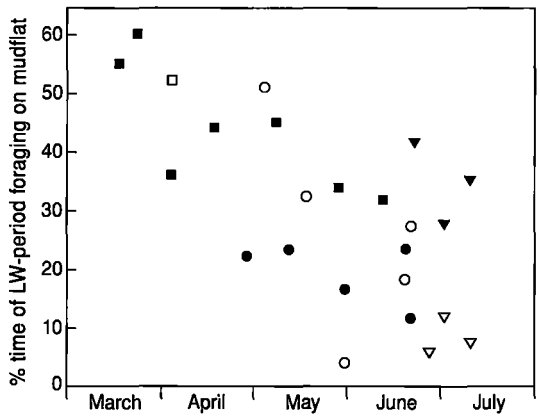


Fig. 15. Time spent on the mudflats during low tide, expressed as a percentage of the total time, in the course of the breeding season. Each dot represents data for one individual followed throughout a tidal cycle in 1984 and different individuals have different symbols.

comparison, this difference was not significant (see legend to Fig. 14). Probably, our analysis suffers from small sample sizes on immatures, which also weakens our conclusion on the seasonal trend. Certainly, when immatures were analysed on their own, it proved impossible to statistically demonstrate a seasonal pattern in their intake rate, even though especially Fig. 14A suggests the presence of such a trend. A more convincing argument that it was not time stress alone that caused the birds to feed faster is therefore the lack of a clear pattern in the speed with which the birds searched for their food (Table 6). Birds hunting for Cockles always walked faster than birds hunting for Mussels, but the variation in the course of the season was minimal, although significant, but in the 'wrong' direction, for Cockles (see legend Table 6).

DISCUSSION

The most striking finding of this study is that Oystercatchers preying on Cockles and Mussels switched to feeding on the smaller sizes of both species during spring. Although the size distribution of the bivalves changed due to growth and, probably, mortality, it was not the case that large sizes disappeared during spring. A similar change in size selection was noted for Oystercatchers feeding on Mussels in the estuary of the Exe (Cayford & Goss-Custard 1990) and for Oystercatchers feeding on an experimental mussel bed on Schiermonnikoog (Ens & Alting 1996) suggesting that it may be a general phenomenon. Since large Cockles and Mussels are the most profitable the change in selection is in stark contrast to optimality models of foraging behaviour that assume that intake rate is maximized. To date, Cayford & Goss-Custard (1990) are the only authors to provide a thorough quantitative test of the optimality model for each month of the season. Their observations match predictions reasonably well, except in April, May and June when the birds take too few of the large size classes. Their calculations include an increase of handling time

with shell size and the observation that for a given size class hammering took more time than stabbing. However, they ignored the possibility that flesh content would also affect handling time. Since we demonstrated that handling time increased when condition was high it is useful to investigate the possible consequences of this phenomenon for their calculations and conclusions. If in the Exe too handling took more time when the bivalves were in good condition, the pronounced seasonal changes in profitability were almost certainly less pronounced. However, as the magnitude of the effect was not large, it is very unlikely that their conclusion that 'weight loss reduced the profitability of larger Mussels in spring but did not affect the relative profitability of different size classes' would be critically affected. Thus, the conclusion remains that the most profitable size classes are dropped from the diet in spring.

Since simple energy maximization cannot explain this behaviour, we must enquire into alternative explanations. Three hypotheses exist, each of which will be discussed in turn:

Seasonal changes in parasite load of the prey Cayford & Goss-Custard (1990) reject the suggestion that it could be due to seasonal changes in the parasite load of the large bivalves on the basis of a personal communication by Dijkema in Meire & Ervynck (1986) that parasite infections are almost absent in Mussels and not related to size. To this we can add that, although we sometimes observed potentially parasitized Cockles 'crawling' on the surface of the mud, there was no striking increase in the number of such Cockles in spring. On the other hand the alternative would seem to be worthy of a more serious investigation, since there are quite a few parasites that Oystercatchers can pick up from eating bivalves (S. LeDrean Quenec'hdu pers. comm.).

Seasonal changes in potential bill damage Another possibility is that the danger of opening large Cockles and Mussels is especially high in spring. One such danger is that the Mussel or Cockle cannot be dislodged from the bill and there exist reports of birds that died as a result (Hulscher 1996). Sutherland (1982) oberved that Oystercatchers rejected Cockles that they had to dislodge from their bill and he showed that the proportion of Cockles that was rejected increased with size. Similarly, Speakman (1984) showed that Oystercatchers did not take Mussels with very large, and therefore strong, adductor muscles. This last explanation only works if adductor mass reaches a peak in spring, i.e. before the peak in biomass content of the bivalves, which is in July on Texel and in November on the Exe (Fig. 18 in Zwarts & Wanink 1993, which is based on Table 1 in Cayford & Goss-Custard 1990). Furthermore, while it is easy to see how stabbing birds might become trapped, it must be unrealistically assumed that hammering birds also run this risk.

Seasonal changes in biochemical composition A third possibility is that the spawning behaviour of the large bivalves might make them unattractive in spring, perhaps due to a change in biochemical composition.

Clearly, these possibilities are all speculative and since they do not exclude each other, they could all be partly true. Although the available data do not allow us to fully resolve the issue we can still ask what changes in the prey choice model are needed to incorporate one or more of the above speculations. One possibility is that the assumption that the rate of energy gain must be maximized is retained, but that one or more constraints are added. For instance, parasitized bivalves are classified as unavailable. Alternatively, we may choose a maximization criterion more closely related to fitness, like minimizing the risk of death. Death may come from disease, predation, major damage of the bill or starvation. We may expect that, more often than not, one risk has to be traded off against another risk. Thus, a foraging strategy based solely on minimizing starvation (which will often, but not always, lead to predictions similar to predictions from maximizing intake rate) can only be expected when the other

risks are very low, or the risk of starvation is very high. Similarly, if the risk of starvation is low, we may expect the other risks to play a more prominent role in the foraging strategy. Below, we will argue that this is the most likely explanation for the change in size selection in spring. Due to an increase in the ambient temperature the expenditure of energy is reduced at that time of year (Kersten & Piersma 1987). Indeed, even Oystercatchers that worked very hard to provision their chicks with food expended only 2.8 × their basal metabolic rate (*BMR*) (Ens *et al.* 1992), whereas the energy expenditure of captive Oystercatchers approached 4 × *BMR* during cold periods in winter (Kersten & Piersma 1987). During incubation, mostly May and June, energy expenditure reaches a seasonal low with 2.1 × *BMR* (Kersten 1996). While energy needs decrease, the rate at which energy can be collected increases. Although we do not yet want to exclude the possibility that breeding Oystercatchers sometimes fed faster as a result of time stress, several lines of evidence suggested that externally determined feeding conditions were important too. Thus, in the course of spring the total food demands decrease, while it is increasingly easy to find food. This allows the birds to achieve very high intake rates even though they ignore the most profitable prey items. Should we really be surprised that in spring Oystercatchers do not adopt a foraging strategy that maximizes the intake rate of food? The answer is a decisive no, and the challenge now consists of quantifying the alternative risks associated with taking particular prey, like the risk of getting parasitized.

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REFERENCES

Beukema J.J. 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 94-107.

Beukema J.J., K. Essink, H. Michaelis & L. Zwarts 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth. J. Sea Res. 31: 319-330.

Cayford J.T. & J.D. Goss-Custard 1990. Seasonal changes in the size selection of Mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*: an optimality approach. Anim. Behav. 40: 609-624.

Ens B.J. 1982. Size selection in mussel-feeding Oystercatchers. Wader Study Group Bull. 34: 16-20.

Ens B.J. & D. Alting 1996. The effect of an experimentally created mussel bed on bird densities and food intake of the Oystercatcher *Haematopus ostralegus*. Ardea 84A: 215-219.

Ens B.J., M. Kersten, A. Brenninkmeijer & J.B. Hulscher 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). J. Anim. Ecol. 61: 703-715.

Ens B.J., T. Merck, C.J. Smit & E.J. Bunskoeke 1996. Functional and numerical response of Oystercatchers *Haematopus ostralegus* on shellfish populations. Ardea 84A: 441-452.

Goss-Custard J.D. & S.E.A. le V. dit Durell 1987. Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on Mussels, *Mytilus edulis*. I. Foraging efficiency and interference. J. Anim. Ecol. 56: 521-536.

Goss-Custard J.D., J.T. Cayford, J.S. Boates & S.E.A. le V. dit Durell 1987. Field tests of the accuracy of estimating prey size from bill length in Oystercatchers, *Haematopus ostralegus*, feeding on Mussels, *Mytilus edulis*. Anim. Behav. 35: 1078-1083.

Hulscher J.B. 1996. Food and feeding behaviour. In: J.D. Goss-Custard (ed.) The Oystercatcher: from individuals to populations: 7-29. Oxford University Press, Oxford.

Kersten M. 1996. Time and energy budgets of Oystercatchers *Haematopus ostralegus* occupying territories of different quality. Ardea 84A: 291-310.

Kersten M. & T. Piersma 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea 75: 175-187.

Kersten M. & W. Visser 1996. Food intake of Oystercatchers *Haematopus ostralegus* by day and by night measured with an electronic nest balance. Ardea 84A: 57-72.

Leopold M.F., C. Swennen & L.L.M. de Bruijn 1989.

Experiments on selection of feeding site and food size in Oystercatchers, *Haematopus ostralegus*, of different social status. Neth. J. Sea Res. 23: 333-346.

Meire P.M. & A. Ervynck 1986. Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable Mussels (*Mytilus edulis*). Anim. Behav. 34: 1427-1435.

Meltofte H., J. Blew, F. Frikke, H-U. Rösner & C.J. Smit 1994. Numbers and distribution of waterbirds in the Wadden Sea: Results and evaluation of 36 simultaneous counts in the Dutch-German-Danish Wadden Sea 1980-1991. IWRB Publication 34/Wader Study Group Bull. Spec. Publ. 74.

Norušis M.J. 1988. SPSS/PC+ V2.0 Base Manual. SPSS Inc., Chicago.

Speakman J.R. 1984. The energetics of foraging in wading birds (Charadrii). Ph.D. thesis University of Stirling, Stirling.

Sutherland W.J. 1982. Do Oystercatchers select the most profitable Cockles? Anim. Behav. 30: 857-861.

Sutherland W.J., B.J. Ens, J.D. Goss-Custard & J.B. Hulscher 1996. Specialization. In: J.D. Goss-Custard (ed.) The Oystercatcher: from individuals to populations: 56-76. Oxford University Press, Oxford.

Swennen C., M.F. Leopold & L.L.M. de Bruijn 1989. Time-stressed Oystercatchers, *Haematopus ostralegus*, can increase their intake rate. Anim. Behav. 38: 8-22.

Van Arkel M.A. & M. Mulder 1975. A device for quantitative sampling of benthic organisms in shallow water by means of a flushing technique. Neth. J. Sea Res. 9: 365-370.

Wanink J.H. & L. Zwarts 1993. Environmental effects on the growth rate of intertidal invertebrates and some implications for foraging waders. Neth. J. Sea Res. 31: 407-418.

Zwarts L. 1991. Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. Neth. J. Sea Res. 28: 231-245.

Zwarts L. & J.H. Wanink 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441-476.

Zwarts L., J.T. Cayford, J.B. Hulscher, M. Kersten, P.M. Meire & P. Triplet 1996. Prey size and intake rate. In: J.D. Goss-Custard (ed.) The Oystercatcher: from individuals to populations: 30-55. Oxford University Press, Oxford.

SAMENVATTING

In de loop van het voorjaar groeien de Kokkels en Mossels in lengte en gewicht (Fig. 4 voor de Mossel en Fig. 6 voor de Kokkel). Ook hun conditie, dat wil zeggen de biomassa bij een bepaalde schelpgrootte, neemt toe (Fig. 5 voor de Mossel en Fig. 7 voor de Kokkel). De schelpgroei stopt in de zomer en in de loop van de herfst en de winter neemt de conditie alsmaar verder af. Wat zijn de gevolgen van deze veranderingen in de loop van het seizoen voor de opname-snelheid en de prooikeuze van de Scholekster? Om te beginnen moeten we er zeker van zijn dat we goede schattingen kunnen maken van prooikeuze, prooigrootte en opnamesnelheid. Voor elke waarnemer werd een ijklijn bepaald, die het verband tussen de werkelijke prooigrootte en de geschatte prooigrootte vastlegde (Fig. 1). Vergelijking van de veldschattingen met metingen middels een weegschaal onder het nest, liet zien dat de veldschattingen zeer betrouwbaar waren (Fig. 2). Wel bleek het nodig zeer korte waarneemperiodes uit het gegevensbestand te verwijderen (Fig. 3). Voor onderzoek naar prooikeuze is prooiprofijt, gedefiniëerd als de opnamesnelheid van biomassa tijdens het bewerken ('hannesen') van de prooi, een belangrijke maat. Hoewel het prooiprofijt wel afhing van de conditie van de mollusken, waren grote Kokkels en grote Mossels in alle gevallen het meest profijtelijk (Figs. 11 t/m 13). Toch verdwenen deze grote prooien geheel uit het dieet in de loop van het voorjaar (Figs. 8 en 9). Ondanks de individuele specialisatie van de Scholeksters (Tabel 3) kon deze trend bij verschillende individueel gemerkte dieren worden aangetoond (Tabel 4). Het negeren van de meest profijtelijke prooien leidde niet tot een daling van de opnamesnelheid. Integendeel, juist in de lente werden de hoogste opnamesnelheden bereikt (Fig. 14). Dit zou kunnen komen omdat de vogels dan nesten moeten verzorgen en weinig tijd hebben om op het wad naar voedsel te zoeken (Tabel 5, Fig. 15). Heel waarschijnlijk is dit niet, omdat ook de onvolwassen vogels een hogere opnamesnelheid hadden in het voorjaar (Fig. 14). Al met al lijkt het er niet op dat Scholeksters proberen een zo hoog mogelijke opnamesnelheid te halen in het voorjaar. Zelfs als ze de grote prooien laten liggen is hun opnamesnelheid nog hoog en hun energiebehoefte is minimaal in die tijd van het jaar. Andere criteria, zoals het risico van snavelbreuk of infectie met parasieten, lijken in het voorjaar een grotere rol te spelen dan maximalisatie van de energiewinst.